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GENETIC STUDIES OF SEVERAL GEOGRAPHIC RACES OF CALIFORNIA DEER-MICE[1]

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SOME of those present may recall a resolution which was adopted at a meeting of the Biological Society of the Pacific, held in Berkeley, in April, 1913, endorsing a project for the study of certain problems, related both to genetics and to geographical distribution. During the same year, the Scripps Institution for Biological Research found it possible to undertake the execution of this project, and the author of the present paper was chosen to carry it out. It is my object to-day to offer a preliminary report upon the results of these studies.

To those who have been so fortunate as to work in fields which yield quicker returns than does that of experimental breeding, it may seem that something more than a "preliminary report" might reasonably be expected after the lapse of a year and a half. If any justification is needed for such seeming slothfulness, I need only remark that my studies have already necessitated the trapping of about 600 living mice, of my chosen species, in four widely distant parts of the state, together with the rearing of several hundred others which were born in captivity; and that I have made measurements of some 500 of these animals, including skeletal measurements of over 400. Care of this rather large family of pets, statistical treatment of the measurements, continuous meteorological observations at several points, and the preparation of a certain number of skins and color photographs, are also to be included in the technique of this project. Without the generous opportunities afforded me by the Scripps Institution, the work could never have been undertaken. And of an importance only second in order I must mention the assistance rendered me throughout these studies by the Museum of Vertebrate Zoology at Berkeley.

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[1] Read before a joint meeting of the American Association for the Advancement of Science (Section F), the American Society of Naturalists, the American Society of Zoologists, the American Genetic Association, and the Eugenic Research Association, at Stanford University, August 4, 1915.

The resolution to which I have referred above formulated four questions which were regarded as especially worthy of consideration in the investigations contemplated. These were:

1. To what extent do influences such as external conditions, the exercise of organs or faculties, etc., which produce modifications of structure or function in the parent, result in bringing about parallel changes in the offspring?

2. If such changes are, in reality, found to reappear in the offspring, do they constitute true examples of heredity?

3. Are the subspecies or geographical races of the systematic zoologists fixed, in the sense of being hereditary, or do the differences by which they are distinguished depend upon conditions which must act anew during the lifetime of each individual?

4. If these subspecific characteristics are actually found to "breed true," do they owe their existence at the outset to "mutations" or to the cumulative effect of environmental influences, or to the mere fact of isolation, acting in some way independently of those influences?

To a large section of experimental breeders in this country, to whom "genetics" is synonymous with Mendelism, such a formulation of problems as this doubtless seems hopelessly archaic. "What is the use of raising all these dead issues," they will ask, "as if Weismann and De Vries and Johannsen had never lived?" And as for the question of subspecies, I suspect that some of our critics would grant them no existence whatever, outside the overwrought imagination of certain taxonomists.

Those, however, who have read dispassionately such able compilations of evidence as are offered us, for example, by Plate[2] and Semon[3] are not likely to fall into the shallow dogmatism which dismisses the whole "acquired characters" question as once for all settled. And those who have taken the trouble to carefully examine a few trays of specimens, representing the subspecies of some widely ranging bird or mammal, will not so readily resort to a subjective interpretation of the phenomenon of geographic variation.

I shall give chief attention to-day to the case of a single species of white-footed mouse, or deer-mouse of the genus *Peromyscus*. According to Osgood,[4] the chief monographer of this genus, the species *maniculatus* comprises about 40 distinguishable geographic races, many of which are so unlike that they would be given full specific rank but for the fact that they intergrade insensibly with one another.

My own special studies have had to do chiefly with those subspecies of *Peromyscus maniculatus* which fall within the limits of the state of California. The first investigations have naturally been directed toward a careful examination of mice representing each of these local races, together with a determination, so far as possible, of the meteorological conditions to which they are subjected in nature. A search for correlations of any sort between structural and environmental differences was, of course, early undertaken.

Mice were collected at four points within the state: Eureka, Berkeley, La Jolla, and in the Mojave Desert near Victorville. At Eureka, Berkeley and Victorville, self-recording instruments (thermographs and hygrographs) have been left in charge of assistants for nine to fifteen months, and recording instruments will be installed at La Jolla this summer. It is planned to continue these records for at least two years. The instruments are placed in positions more nearly representing the natural environmental conditions of the animals than is customary for regular Weather Bureau stations (*e. g.*, in a redwood forest on the outskirts of Eureka).

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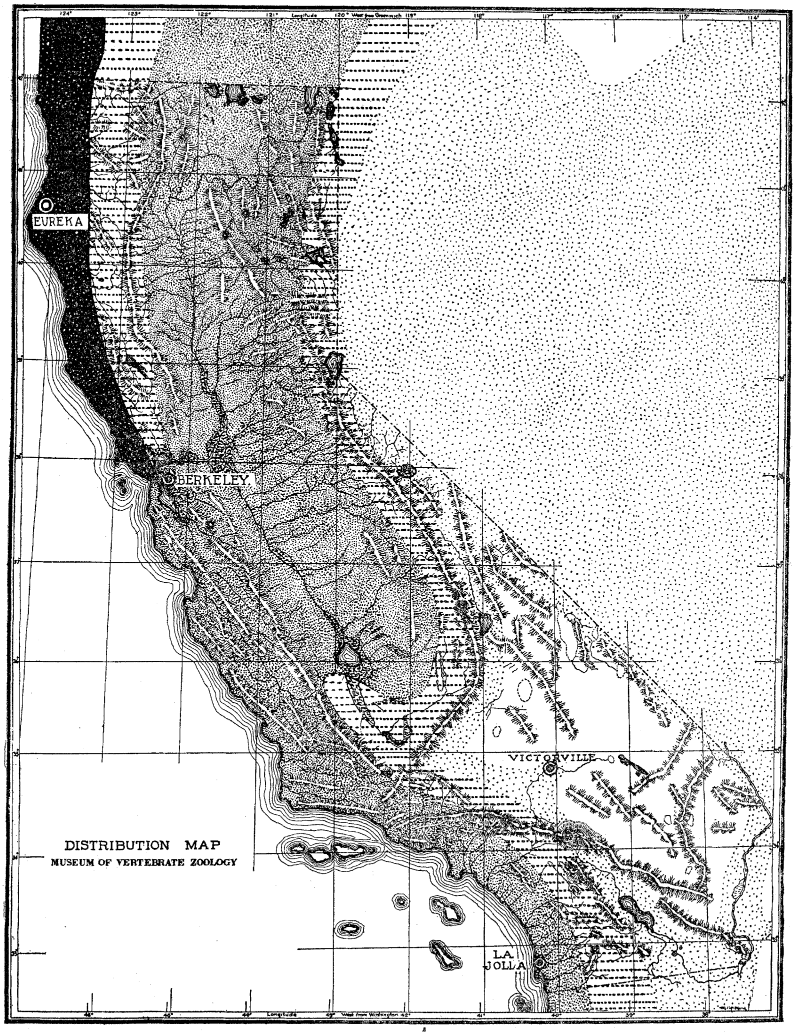
[2] "Selektionsprinzip," vierte Auflage, Engelmann, 1913.

[3] "Das Problem der Vererbung 'erworbener Eigenschaften,' " Engelmann, 1912.

[4] "Revision of the Mice of the American Genus *Peromyscus*," U. S. Department of Agriculture, Biological Survey, 1909.

The Eureka mice are assigned to the subspecies "*rubidus*," those from the desert to "*sonoriensis*," while those



Distribution of the Subspecies of *Peromyscus maniculatus* in California and Nevada, Based upon the Distribution Map of Osgood (1909). The heaviest shading denotes the range of *P. m. rubidus*, the intermediate shading that of *gambeli*, the lightest that of *sonoriensis*. Areas of intergradation between two races are indicated by dotted lines.

from Berkeley and La Jolla are assigned by Osgood to the same subspecies "*gambeli,*" although, as I shall point out, there are certain slight differences of type between the two.

Now, as to characters, I have made 14 measurements of each completely measured mouse. Certain color characters, not capable of quantitative expression, have also been taken into consideration. I shall first consider the measurable parts. I must introduce this discussion by stating that my comparisons are entirely between animals of the same body length. When I say that *P. m. rubidus* has a longer tail than *sonoriensis,* I mean that this is true for mice of equal size. Owing to the impracticability of giving you a mathematical justification of all the steps which I have taken, I will ask you to credit me with a knowledge of the more elementary statistical methods.[5] I must also explain that I have thus far failed to kill and measure many animals from which I shall before long have full data. At present these are being retained for breeding purposes. Hence my series of measurements, in certain cases, is very small.

To present these subspecific characters briefly, I may say that, in respect to tail and foot length, *rubidus* stands in a class by itself. It does not require the trained eye of a systematist to detect the fact that this northern race has conspicuously longer tail and feet. In the case of the tail, this difference is due almost wholly to a difference in the length of the individual vertebræ, not to an increase in the number of these.[6] The other three races (*sonoriensis* and the two lots of *gambeli*) show no statistically certain differences in either of these characters. *P. m. rubidus* likewise has a significantly greater skull length and probably also a greater cranial capacity.[7]

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[5] The detailed data must be deferred until a somewhat later stage of the work. Some of these were presented to the meeting in the form of graphs.

[6] The same was found to be true of the artificially induced modifications in tail length, described by me elsewhere for white mice.

[7] Determined by suitably cleaning and then desiccating the skulls, and weighing the volume of mercury which just filled the cranial cavity.

The La Jolla race of *gambeli* seems to fall second in the list in this regard.

The only significant difference in ear length is that between the two races of *gambeli,* the La Jolla stock having noticeably longer ears than the Berkeley stock, while *rubidus* and *sonoriensis* appear to be intermediate in this respect.

As regards color differences, these relate chiefly (1) to the depth of shade, and (2) to the extensity of the pigmented areas. A careful comparison of large numbers of the Berkeley race (*gambeli*) and the desert race (*sonoriensis*) revealed at least ten recognizable differences of this class, though in many cases these were merely different expressions of the same fundamental difference. None of the distinctions between these two races are absolute ones, holding between any two individuals of the contrasted races. Rather they are distinctions "on the whole," expressed by differences of mode or mean. Taken collectively, however, it is likely that these characters form an ensemble sufficiently distinct to reveal the identity of practically every specimen.

The most widely separate of the races, in respect to color, are *rubidus* and *sonoriensis,* the former race being very much darker than the latter. The two lots of *gambeli* occupy intermediate positions between the others.

METEOROLOGICAL DATA AT FOUR CALIFORNIA STATIONS.

	Temperature (°F.)		Humidity		Rainfall
	Annual Mean	Annual Range	Annual Mean	Daily range	Annual total
Eureka[8]	51.6	8.9	86	Very small	45
Berkeley	56.1[9]	14.4[9]	83[8]	Small	26[9]
La Jolla (San Diego)[8]	60.6	14.7	75	Small	10(−)
Mojave Desert	(Mojave)[8] 63.6	(Mojave)[8] 40.4	(Victorville)[10] 45±	High	(Victorville)[11] 6

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[8] U. S. Weather Bureau.

[9] University Observatory.

[10] Computed from observations during present experiments (only one half year at this station).

[11] Rain-gauge records of Mr. Reginald Frost.

Now do we find any instances of correlation between these differences of structure or color and differences in environmental conditions? The most conspicuous of the structural differences relate to the greater length of the tail and foot of the Eureka race (*rubidus*) as compared with any of the other three races here considered. It is of considerable interest to note that there is here an increase in the length of these appendages as we pass to the northward, a circumstance which is still further emphasized by the condition of certain Alaskan subspecies. In fact, so far as these coastal subspecies of *Peromyscus* are concerned, there seems to be, within certain limits, a reversal of Allen's principle of the shortening of "peripheral parts" as we pass from south to north. The facts here revealed are likewise out of harmony with my own experimental results from white mice, which showed conclusively that low temperature and high humidity led to a decrease, rather than an increase in the length of the tail and foot.[12] A little later I shall point out the pronounced effect of certain other artificial influences upon the length of these appendages in *Peromyscus*, though I must admit that these later experimental results furnish no more satisfactory clue to the origin of these differences in nature.

On the whole, then, these preliminary researches do not offer much ground for believing that the differences found in the tails and feet of these wild races of *Peromyscus* result directly from any differences in environmental stimuli, or for expecting that they will respond appreciably to artificial climatic changes.

Passing to color differences, we seem to have here a good illustration of that correlation between atmospheric humidity and depth of pigmentation which has long been recognized to hold for mammals, birds and some other animals. If we arrange our four environments in ascending order with respect to their atmospheric humidity

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[12] Cf. *Journal of Experimental Zoology*, April, 1915, and earlier papers therein cited.

(the same order holds with respect to their rainfall), we have the series: (1) Victorville, (2) La Jolla, (3) Berkeley and (4) Eureka. Correspondingly, the desert mouse (*sonoriensis*) is the palest of the lot, while the La Jolla mouse, the Berkeley mouse and the Eureka mouse follow in the order of increasing pigmentation. This relation, when viewed in connection with a wide range of known facts, and with certain experimental data to be noted later, can hardly be regarded as accidental. Any exact quantitative determination of the density of pigmentation would of course be difficult, and it has not yet been attempted. But the width of the dorsal median stripe of the tail is found to serve in some measure as an index of the extension of the darkly pigmented areas. It is interesting to note, in order of increasing width: *sonoriensis* (28 per cent.), *gambeli* (32 per cent.) and *rubidus* (43 per cent.). (The *gambeli* considered are from La Jolla.)

Let us grant then, provisionally, some sort of causal relationship between atmospheric humidity and the quantity of pigment in the hair or feathers. Now, aside from our ignorance of the physics and chemistry of the processes here involved, there is still a most important biological question left unsolved: Are these differences in pigmentation between the various geographical races germinal in their origin or are they purely somatic and individually acquired?

It was but a few years ago that Mr. J. A. Allen[13] was shocked by the very moderate suggestion of President Jordan's[14] that perhaps some of our subspecific differences were "ontogenetic," and not racially fixed. Mr. Allen was shocked, though unable to offer any really substantial evidence in reply. In this uncertainty over so elementary a matter of fact, everybody suggested decisive experiments for some one else to perform, but somehow no one seemed disposed to perform them. At least the question of the fixity of the subspecies of mammals and birds has, to my knowedge, never before been put to experimental test.[15]

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[13] *Science*, January 26, 1906.

[14] *Science*, December 29, 1905.

Now, in view of the subject matter of the present paper, it would ill become me to underrate the value of such tests. But I think that I have had enough to do with the experimental method in zoology to make me realize its rigid limitations. It is seldom indeed that we are able to perform a really crucial experiment and to obtain unequivocal results. Moreover, the mills of the gods grind slowly, while the single human life is short.

I am therefore disposed to attach considerable importance to what have been called "Nature's experiments." Certain of these have been cited by Grinnell and Swarth[16] in their bearing on the subspecies question. For example, two well-marked local races or subspecies of song-sparrow occur in southern California, on opposite sides of the high mountain range which divides the coastal plain from the desert interior. These races are separated nearly everywhere by the mountain barrier, but at certain points passes through the latter occur, permitting of migration from one side to the other.

Now these authors find localities in which the coast form of song-sparrow has penetrated, for considerable distances, into the desert and has become established there. Nevertheless, these invaders, which have perhaps been exposed for many generations to the desert atmosphere, have retained the darker pigmentation and other characteristics proper to the coastal plain.

Again, both Grinnell and Taylor[17] have taken specimens of *Peromyscus maniculatus*, which they believe to be typical representatives of the desert race *sonoriensis*, high up in the mountains of California and Nevada. These points are continuous with the main habitat of the subspecies in the desert lowlands and plateaus, in the sense that no abrupt barriers intervene, but they present very great differences in climate and vegetation.

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[15] It is interesting to note that the often cited case of the Porto Santo rabbit has been recently put in quite a new light by the investigations of G. S. Miller, who finds that this transplanted race is merely the *unmodified* rabbit of southern Europe. (Catalogue of the mammals of western Europe, in the British Museum, London, 1912.)

[16] University of California Publications in Zoology, Vol. 10, No. 9, 1913.

[17] University of California Publications in Zoology, Vol. 7, No. 7, 1911.

Facts of this sort—"natural experiments," as we may call them—seem to show that these subspecific differences manifest themselves in a large degree independently of climatic conditions, in other words, that they are of germinal rather than of somatic origin.

But these "natural experiments" are not entirely conclusive, for we can never be quite certain what the actual condition are which Nature has imposed in a given case. Granting that these darker song-sparrows in the desert are actually invaders from the coastal plain, we have no means of knowing how long they have been exposed to the desert conditions. Also is it definitely known that their restricted habitat in certain portions of the desert does not agree with their original habitat in respect to those factors which are really essential in determining their characteristic coloration?

My own first attempt at transplantation consisted in bringing a considerable number of specimens of *P. m. sonoriensis* from the vicinity of Victorville to Berkeley.[18] At the latter point, the mice were kept in cages, freely exposed to the air, and under atmospheric conditions as nearly natural as possible. For control, numbers of the Berkeley race were reared in neighboring cages. The result of this experiment I can state briefly: *Neither the originally introduced animals nor their offspring, nor their grandchildren, have thus far shown any perceptible approach to the local type. They are still obviously of the sonoriensis race.* If there is any tendency for these mice to be modified in the direction of *gambeli*, this tendency is not sufficiently great to be detected through any mere gross comparison, based upon qualitative characters. Unfortunately, these two races differ significantly in color characters only, so that an exact quantitative test of this question is not here possible. But I am now rearing *P. m. rubidus* at La Jolla, an experiment which would seem to be much more promising of decisive results than the one just described.

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[18] The contrast between the climatic conditions at the two points is indicated, to a certain extent, in the foregoing table. But this does not show one of the most characteristic differences, namely, the relatively enormous diurnal fluctuations of temperature and humidity in the desert, as compared with those in the coastal region.

Enough has been done, therefore, to prove that the color differences between *sonoriensis* and *gambeli* are at least in a large degree germinal and independent of environmental influences acting during a single lifetime. Whether or not they are *wholly* germinal, and if so, whether they can resist change for an indefinite number of generations, remains to be learned. Suppose that we had a shifting of the mean to the extent of one per cent., or even ten per cent., in the direction of *gambeli*. Amid all the natural variability, we certainly should not be able to detect such a change with the unaided eye.

In interpreting the facts that I have offered as to the relative fixity of these color differences of *Peromyscus*, we should have due regard for various other experiments which show that environmental influences may produce notable changes of coloration in the lifetime of an individual. As especially comparable with these tests of my own, though differing completely in the outcome, may be cited the experiments of Beebe.[19] This author produced a marked increase of pigmentation in the feathers of three species of birds by rearing them in an atmosphere of abnormally high humidity.

Beebe's experiments seem to show that pigmentation may in some cases be altered during a single lifetime by changes of humidity. The generally known facts of geographic distribution show that there is in nature a distinct correlation between pigmentation and humidity. My own experiments show that these geographic differences of pigmentation are capable of being relatively fixed germinally. Bringing these three sets of facts together, they are, in my opinion, most readily harmonized on the assumption that the direct effects of humidity upon the organism may finally become fixed through heredity.[20] But I grant that this assumption is as yet far from proved.

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[19] *Zoologica*, N. Y. Zool. Soc., Sept. 25, 1907.

A study of the effects of captivity forms a new line of inquiry which was hardly considered when the present researches were undertaken. For some reasons, however, this line of investigation now seems quite as promising as the search for climatic effects. In the first place, my comparatively meager results in this field already reveal striking differences between the wild stock and the individuals of the first generation reared in captivity. These differences relate to absolute size (the domesticated generation being smaller), to length of tail and foot (both shorter in the domesticated) and to the length of the femur and the pelvis, which differ in the same direction. In the case of the femur, in particular, the differences are striking, even upon the most casual inspection, and they are absolutely certain statistically. They hold for both sexes and for both of the subspecies which have thus far been tested in this regard. Thus far, no certain effects upon the cranial capacity of the captive lots have been detected.

Such differences as those found probably have nothing to do with the direct effects of external conditions, but are due to the *activities* of the animal. For this reason, they are of much higher value as a test of the Lamarckian principle, which could help us most in explaining the perfecting of active parts through use or of their degeneration through disuse.

The experimental results just referred to suggested the possibility that some of the differences found to occur in nature might have had a functional basis. The larger feet and tail of *P. m. rubidus,* for example, might be attributed to its (assumed) greater activity. Unfortunately for this theory, the pelvis and femur of *rubidus* is no greater (slightly smaller, it would seem) than in the other races. Had the enlargement of the foot been due to greater functional activity the skeletal parts named would probably have also undergone an increase in size.

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[20] Whether this results from ''somatic'' or ''parallel induction'' need not concern us here.

From a series of measurements upon the skeletons of wild and domestic fowls and rabbits, Darwin inferred a relative decrease in the size of the wings of the former and of the cranial capacity of the latter, under the influence of domestication. These conclusions may well be true, but the evidence offered seems to be open to several objections. (1) They are based on too small numbers and lack the precision demanded by modern statistical work. (2) We can only infer the exact nature of the wild stock from which the domesticated races are descended. (3) We can not judge of the extent to which artificial selection may have played a part in bringing about these differences. It was perhaps considerable. (4) We do not know how much of this modification results from use or disuse during the animal's own lifetime. It might be contended that the change was not congenital at all.

Lapicque and Girard have, in the main, demonstrated a smaller cranial capacity in domesticated animals as compared with wild ones, but aside from the more rigorous statistical methods employed by these authors, the biological significance of their results is open to the same objections as I have stated in the case of Darwin's.

Hatai[21] has shown that the albino rat has a smaller brain than the wild Norway rat, when individuals of the same size are compared. This proves nothing definite, however, as to the effects of domestication, a fact which the author recognizes. The deficient brain of the albino may have been part of the same mutation which brought about the albinic condition. Or it may have resulted in part from the selection of tamer individuals. Or the difference between the two races may be purely ontogenetic. Indeed, Donaldson[22] seems to have demonstrated the effects of exercise upon the weight of the nervous system of the rat.

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[21] *Anatomical Record,* Vol. 3, 1909, p. 245.

By taking a known stock of wild mice and measuring each successive generation reared in captivity, and by being careful to avoid selection, it would seem that the foregoing ambiguities of interpretation might in a large degree be obviated. It is possible, therefore, that this phase of the subject deserves quite as much attention as the problems relating to the physical environment and the distribution of subspecies.

Hybridization has thus far failed completely between *rubidus* and *gambeli* (48 matings). The Berkeley *gambeli* has, however, been successfully crossed with *sonoriensis* and some young of an F_2 generation have already been obtained. Owing to the intergrading and widely overlapping character of the differences between these two races, it does not seem likely that they will lend themselves well to Mendelian analysis. But it would be idle for me to discuss the results of these crosses at the present stage of the experiments. Further attempts will, of course, be made to obtain hybrids between the more widely separated races.

(Since writing the foregoing, several successful matings between *rubidus* and *sonoriensis* have been effected.)

[22] *Journal of Comparative Neurology*, Vol. 21, No. 2, 1911.